



Floral morphology, nectar production, and breeding systems in
Dudleya subgenus *Dudleya* (Crassulaceae)

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Abstract. Floral morphology, nectar production, and breeding systems of 21 taxa in *Dudleya* subgenus *Dudleya* suggest three reproductive strategies. Most species—13 of those examined—have 1–15% auto-fertility (defined as the proportion of seed set by self-pollination in the absence of pollinators) and produce nectar with about 2–5 mg sugar per flower. These species, which are predominantly coastal in distribution, have dense inflorescences of yellow flowers and appear to be pollinated primarily by bees and long-tongued flies. Increased seed set and seedling vigor with cross-pollination select for outcrossing in these species. A second group of three species has long-tubed, frequently pendent, red flowers in very open cymes, high auto-fertility (about 40–60%), and abundant nectar—yielding 5–12 mg sugar/flower. Ranging from hills near the coast to desert mountains, these species are hummingbird-pollinated. The remaining three species (one with three subspecies) have short-tubed flowers in dense cymes, high auto-fertility (25–50%), and nectar production of less than 2.5 mg sugar/flower. These species are typically montane and occupy habitats with shorter and less reliable growing seasons than are usual for the genus. Environmental unpredictability and pollinator unreliability may explain the apparent trend toward autogamy in the third group and the high auto-fertility of the hummingbird-pollinated species. Because flowers are protandrous, even species with high auto-fertility maintain the ability to outcross if pollinators are available.

INTRODUCTION

The genus *Dudleya* (Crassulaceae) consists of about 40 species of succulent rosette perennials of western North America (Moran 1951, 1959). Subgenus *Dudleya* is the most diverse (about 25 species) and most widespread of the three subgenera. The greatest diversity is in coastal and insular southern California and Baja California, although the subgenus extends from the Cape Region of Baja California to coastal southern Oregon and inland to southern Nevada and central Arizona, spanning an altitudinal range from sea level to 2750 m. Habitats include coastal bluffs, montane canyons, and slopes of desert mountains. About half the species are narrow endemics, many of them insular; the remainder are widespread. Except in a few species of coastal northern Baja California, distributions are mostly patchy, with populations commonly small and well isolated.

Given the great diversity of habitat and population structure of its species, *Dudleya* might be expected to vary in 1) breeding systems, 2) pollination syndromes, and 3) reproductive strategies. Some aspects of pollination biology have been shown to vary within groups of related plants, e.g., at the family level in Polemoniaceae (Grant and Grant 1965) and Bignoniaceae (Gentry 1974), and at the generic level in *Agave* (Schaffer and Schaffer 1977), *Leavenworthia* (Lloyd 1965, Solbrig 1976, Solbrig and Rollins 1977), *Pedicularis* (Sprague 1962, Macior 1968, 1970), *Rhododendron* (Stevens 1976) and *Trichostema* (Spira 1980). Yet, except in Spira's study, variation in all three aspects has not been examined in a single genus.

METHODS

We studied floral morphology, nectar production, and breeding systems in field-collected plants grown in a glass-topped screenhouse at Rancho Santa Ana Botanic Garden, Claremont, California. Localities of the populations studied are listed in the Appendix. As noted below, we also made some field measurements of nectar production. We also observed pollinators on several species, although most observation periods were relatively short.

We determined nectar volume by extracting all nectar from a flower with a volumetric (5- μ l or 10- μ l) capillary tube. Upon sampling, we immediately measured the concentration (in mg sucrose equivalent/mg solute) of sugar in the extracted nectar with a hand-held Bausch & Lomb sucrose refractometer. We converted concentrations to mg sucrose equivalent/ml solution using Table 88 in the 59th edition of the Handbook of Chemistry and Physics (1978–1979:D-308) and then calculated total sugar by multiplying concentration by nectar volume (Bolten et al. 1979).

To determine phenology of nectar production and variation in nectar concentration and volume with flower age, we sampled flowers at different stages of anthesis. The first season, we recorded the relative age of each flower. The second season, in order to obtain measurements on the basis of absolute time, we sampled flowers at daily intervals after they opened. Because sampling often damaged the flower, we could not reliably resample the same flower. Instead, for each time period, we sampled 10 flowers, chosen from several plants.

On each flower sampled for nectar, we measured the length of the corolla tube, that portion of the corolla in which adjacent petals are fused; sample sizes ranged from 50–80 flowers. We also recorded flower color and positions of anthers and stigmas.

To determine the breeding systems of the different species, we mechanically self-pollinated some flowers, mechanically cross-pollinated others, emasculated others in bud, and left others untouched. We allowed fruits to mature on the plants but removed them before dehiscence. Percentage seed set was determined by dividing the number of developed seeds by the total number of ovules. Unfertilized ovules were small and withered, making them easy to distinguish from the larger plump seeds. Typically, three flowers from three different plants were included in each treatment.

For six species, we compared viability and seedling vigor of seeds from self-pollinated and cross-pollinated flowers by planting 30 seeds from each treatment and counting the number of seedlings at three and seven weeks after sowing.

POLLINATORS

Floral morphology suggests that there are two different groups of pollinators. In all species of subgenus *Dudleya*, the petals are essentially erect, with the overlapping edges usually closely appressed above the corolla tube (Fig. 1). In the relatively small flowers of most species (7–15 mm long), nectar is available to small bees and flies that can crawl into the corollas, and to larger insects with moderately long tongues. These species primarily have yellow to orange flowers, many with ultraviolet reflectance patterns (T. W. Mulroy, *pers. obs.*), borne erect in more or less flat-topped inflorescences that would serve well as insect landing platforms (Figs. 1 and 2A). Apparently the genus has little ability to produce a floral scent: only three species, none of them in subgenus *Dudleya*, produce any aroma (Moran 1951, 1959; *pers. obs.*).¹ We have observed bees of eight genera and occasional butterflies visiting *Dudleya* flowers (G. A. Levin in prep.); Moldenke (1976) listed bees in the genera *Bombus* and *Anthophora* as important pollinators of *Dudleya*.

Three closely related species, *D. arizonica*, *D. anthonyi*, and *D. pulverulenta* (Fig. 2B, C), appear to be hummingbird pollinated. The latter two, in particular, possess a

¹ Although Johansen (1935) reported that flowers of *D. echeverioides*, now regarded as a synonym of *D. greenii*, have an odor resembling woodland violets, neither we nor Moran (1951) has been able to detect any floral fragrance in *D. greenii*.

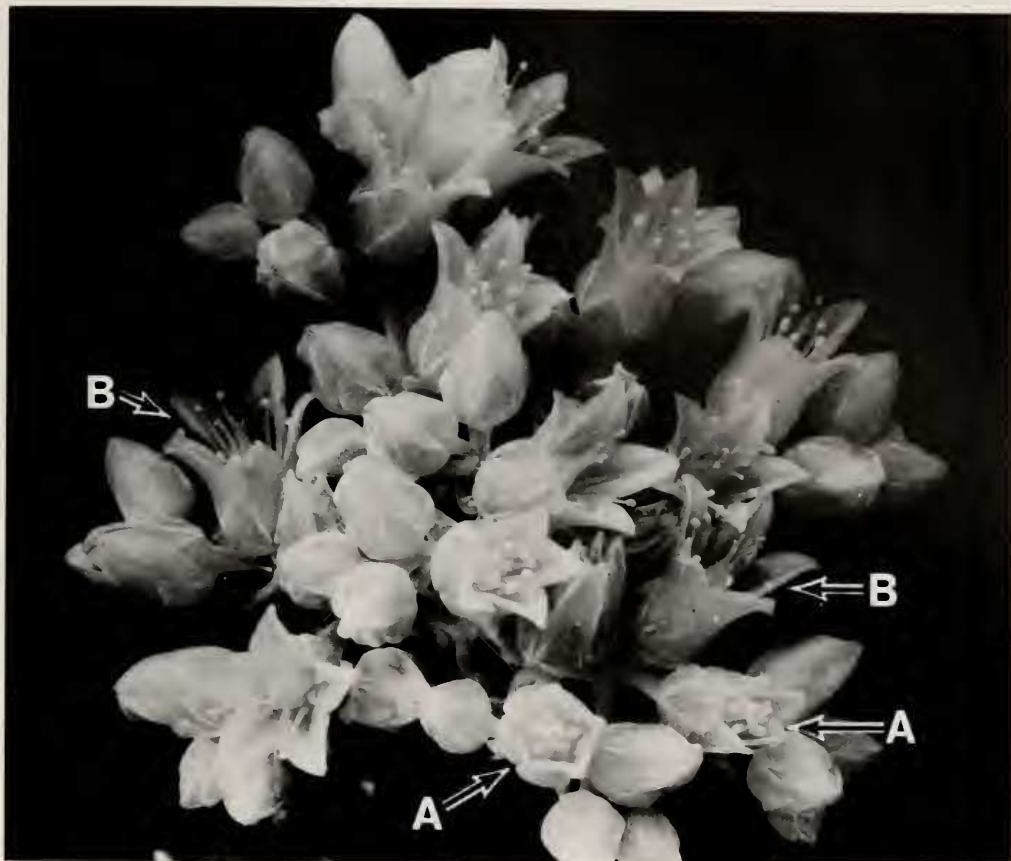


FIGURE 1. Inflorescence of *Dudleya greenei*. Arrows labeled A indicate young flowers (1–2 days old); the anthers have dehisced and are positioned toward the center of the corolla. Arrows labeled B indicate older flowers (3–5 days old); the styles have elongated, positioning the now receptive stigmas near the mouth of the corolla, and the anthers are positioned near the edge of the corolla. As the flowers age further, the anthers will again move toward the center. (Photo by Reid Moran.)

suite of characteristics associated with hummingbird pollination (Faegri and van der Pijl 1979, Grant and Grant 1968). Their corollas are 1.5–2 cm long, fused about 1 cm, and colored deep red. The flowers are pendent on long, slender pedicels, becoming erect in fruit. The inflorescences of these species are typically more open than in the remainder of the species. *Dudleya arizonica* also has red flowers, but they are somewhat smaller (1.2–1.4 cm long) and erect in more dense inflorescences. By probing flowers with a dead hummingbird (sp. indet.), we found that hummingbirds could effect pollination while feeding, and we have observed them foraging on *D. pulverulenta* and *D. arizonica*. We also observed hummingbirds visiting *D. brittonii*, *D. cymosa cymosa*, and *D. ingens*, species that are better adapted for bee pollination (G. A. Levin in prep.). Grant and Grant (1966) reported hummingbirds visiting *D. cymosa minor* and *D. lanceolata*, and Moldenke (1976) considered hummingbirds to be the principal pollinators of *Dudleya*, although he did not indicate which species he observed.

NECTAR PRODUCTION

Phenology.—In *Dudleya*, the nectaries are located at the base of the gynoeccium. The flowers are strongly protandrous (Fig. 1), and nectar volume and concentration are correlated with the age of the flower (Fig. 3). No nectar is produced before the anthers release pollen. Following anther dehiscence, nectar is secreted rapidly and

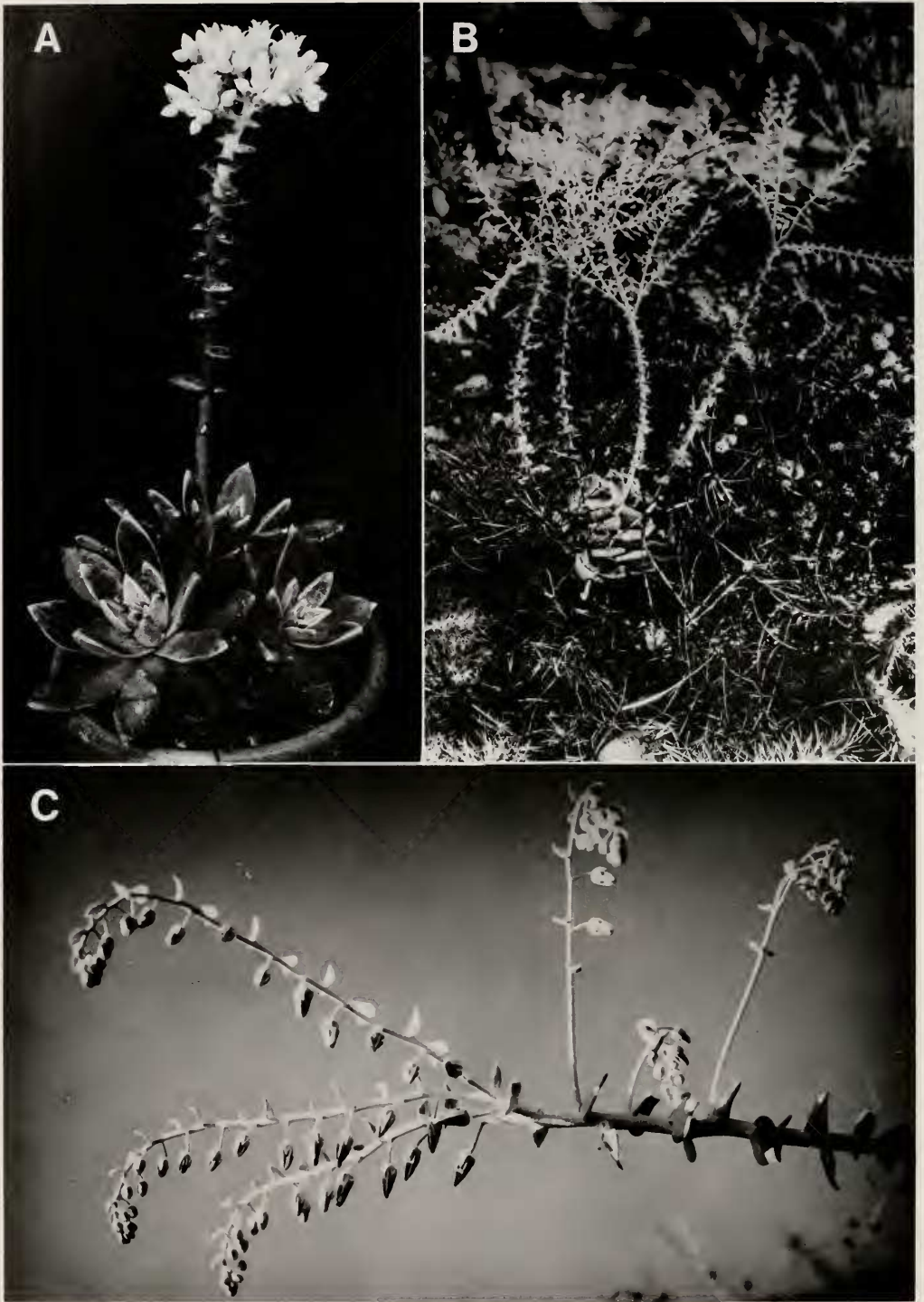


FIGURE 2. A—Flowering plant of *Dudleya greenei*, typical of bee-pollinated *Dudleya* species (photo by Reid Moran). B, C—Flowering plant and inflorescence, respectively, of *Dudleya pulverulenta*, typical of hummingbird-pollinated *Dudleya* species.

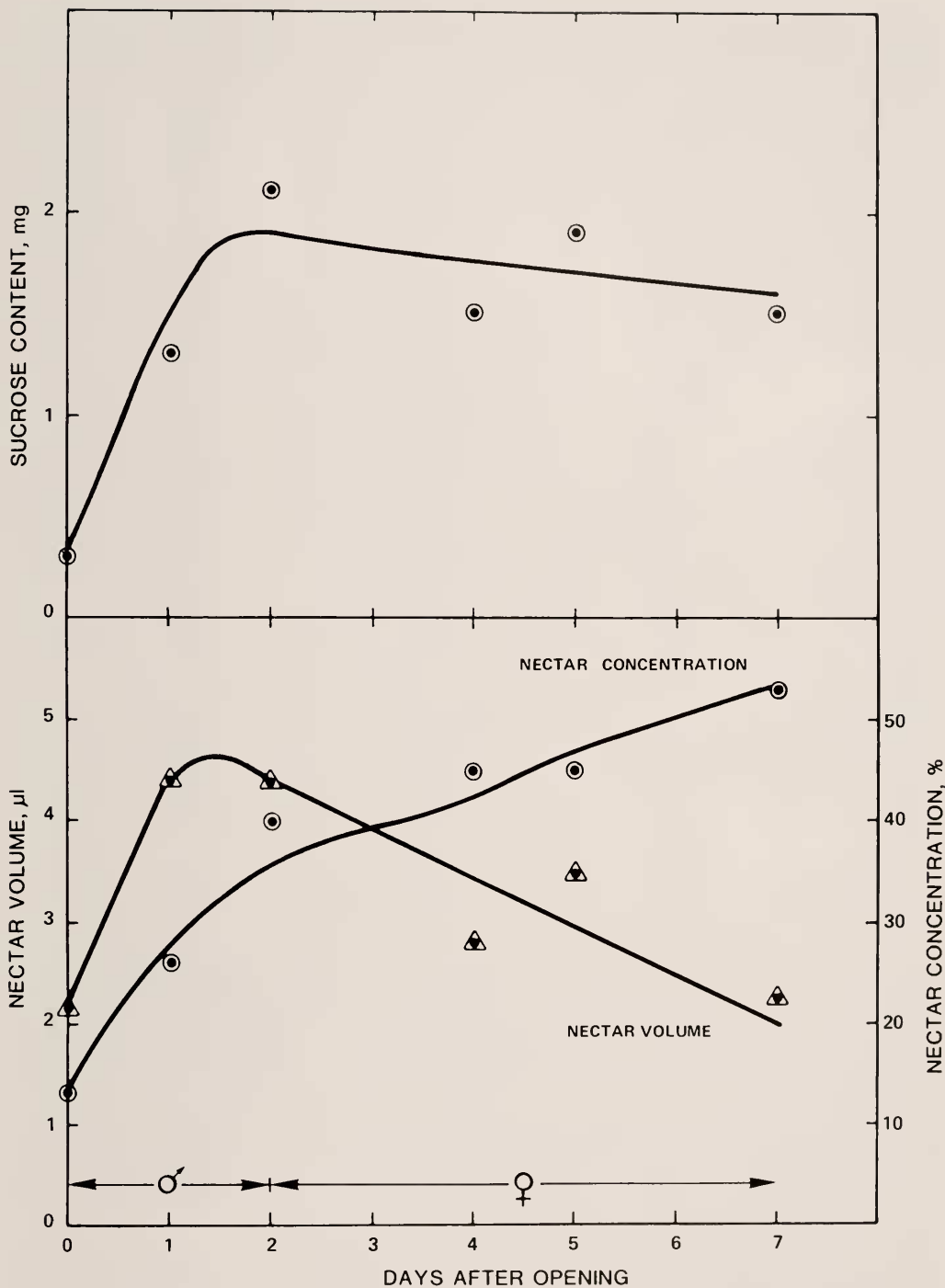


FIGURE 3. Phenology of nectar production in *Dudleya nubigena*, representative of the typical pattern in subgenus *Dudleya*. Points indicate mean values. Concentration is in g sugar/100 g solution. Flowers are protandrous; stigmas become receptive on day 2.

TABLE 1. Characteristics of nectar production and corolla tube length in *Dudleya* subgenus *Dudleya*. "Maximum" denotes the mean of the three highest measurements of that characteristic. Concentration is in g sucrose equivalent/100 g solution. Energy content is based on 4 cal/mg sugar (Heinrich 1975).

<i>Dudleya</i> species	Maximum volume μl	Minimum conc. %	Conc. at max. vol. %	Maximum sucrose content mg	Maximum energy content cal	Corolla tube length mm
<i>abramsii</i>	trace	—	—	—	—	1.4
<i>acuminata</i>	4.8	36	51	3.4	13.6	4.2
<i>albiflora</i>	4.2	37	42	2.1	8.4	4.3
(2 populations)	5.6	—	46	4.1	16.4	5.0
<i>anthonyi</i>	14.0	34	40	9.5	38.0	6.0
<i>arizonica</i>	9.2	—	31	4.8	19.2	5.7
(3 populations)	5.6	29	40	2.9	11.6	6.2
	16.0	25	35	7.8	31.2	7.0
<i>bettinae</i>	1.8	36	48	1.1	4.4	1.0
<i>brittonii</i>						
glaucous form	3.4	40	51	2.3	9.2	2.9
(2 populations)	7.4	—	50	4.7	18.8	3.2
green × glaucous	6.8	—	26	4.1	16.4	3.8
<i>caespitosa</i>	11.5	—	51	7.2	28.8	2.4
(2 populations)	11.5	—	34	4.6	18.4	2.4
<i>cultrata</i>	3.1	32	37	1.6	6.4	1.9
(2 populations)	8.9	—	30	4.8	19.2	3.7
<i>cymosa cymosa</i>	2.8	35	38	1.1	4.4	1.1
<i>c. marcescens</i>	3.7	26	40	2.0	8.0	1.1
<i>c. ovatifolia</i>	4.8	22	32	2.4	9.6	1.6
<i>gatesii</i>	13.5	32	44	6.8	27.2	6.1
<i>greenei</i>	4.7	51	58	3.5	14.0	1.3
<i>ingens</i>						
coastal form	4.0	29	51	2.3	9.2	2.0
(2 populations)	12.0	—	33	5.9	23.6	5.0
inland form	7.3	—	49	4.8	19.2	5.0
<i>lanceolata</i>	9.0	25	42	4.4	17.6	2.3
<i>linearis</i>	2.3	27	44	1.3	5.2	2.0
<i>nubigena</i>	5.0	24	28	2.2	8.8	3.2
<i>parva</i>	trace	—	—	—	—	1.9
<i>pulverulenta</i>	44.0	23	25	14.3	57.2	7.7
(2 populations)	32.1	20	30	12.5	50.0	8.0
<i>saxosa saxosa</i>	5.7	32	38	2.5	10.0	1.8

collects in the base of the corolla tube. Volume and concentration increase throughout the male phase of anthesis, reaching maximum volume soon after the stigmas become receptive. Thereafter, nectar volume tends to decrease and concentration continues to increase, probably because of a cessation or attenuation of nectar secretion and evaporation of water from the nectar.

Sugar content, like nectar volume, increases rapidly through the male phase and reaches a maximum after the stigmas become receptive (Fig. 3). Thereafter sugar content remains essentially constant, again suggesting that nectar secretion had ceased. Other genera have similar patterns of age-related nectar production (Anderson 1976, Carpenter 1976, Feinsinger 1978, Pyke 1978, Cruden et al. 1983).

The phenology of nectar production in *Dudleya* is highly economical. During the male phase of anthesis, visiting foragers pick up pollen on their bodies and may carry it to other flowers. Pollinators continue to be attracted to a flower until stigmas are receptive, but soon thereafter no more nectar is produced to reward their visits. The flower will probably have been pollinated by this time, so further visits are unnecessary. Within 24 h following pollination (provided the stigmas are receptive), the flower closes. However, unpollinated flowers remain open for up to five days after the stigmas become receptive, and because no morphological changes are associated with the cessation of nectar production, it is likely that pollinators will continue to be attracted to unpollinated flowers by previously accumulated nectar.

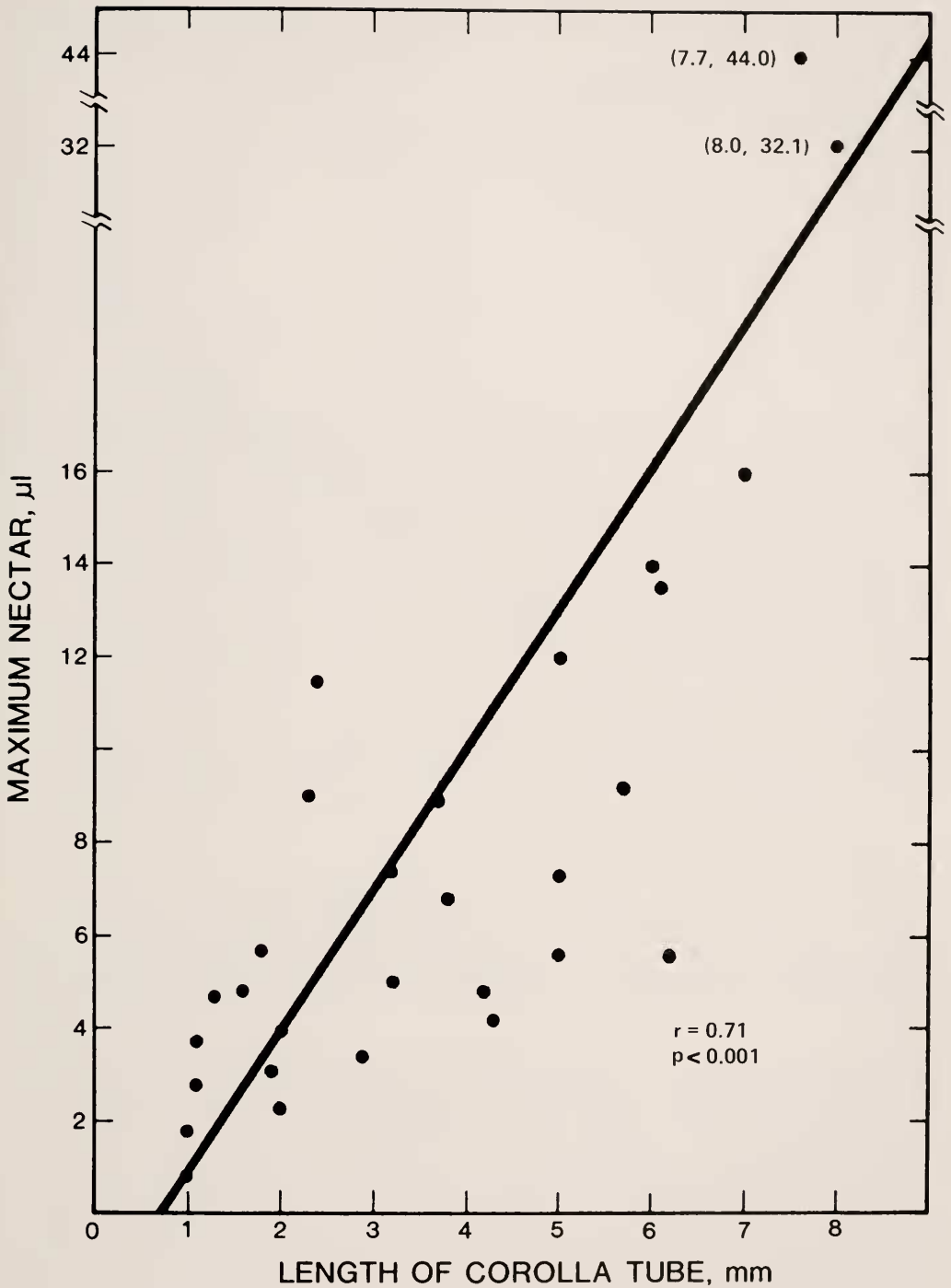


FIGURE 4. Relationship between maximum nectar volume and corolla tube length in *Dudleya* subgenus *Dudleya*. Each point represents one population. Linear correlation of $r = .71$ is significant ($P < .001$).

Environmental factors affect nectar production in *Dudleya*. Cool, cloudy weather reduces the rate of secretion; in some cases only a trace of nectar accumulated in flowers open for three rainy days. Similar meteorological effects on nectar production have been observed in alfalfa (Pederson 1953, Walker et al. 1974) and *Ipomopsis* (Pleasant

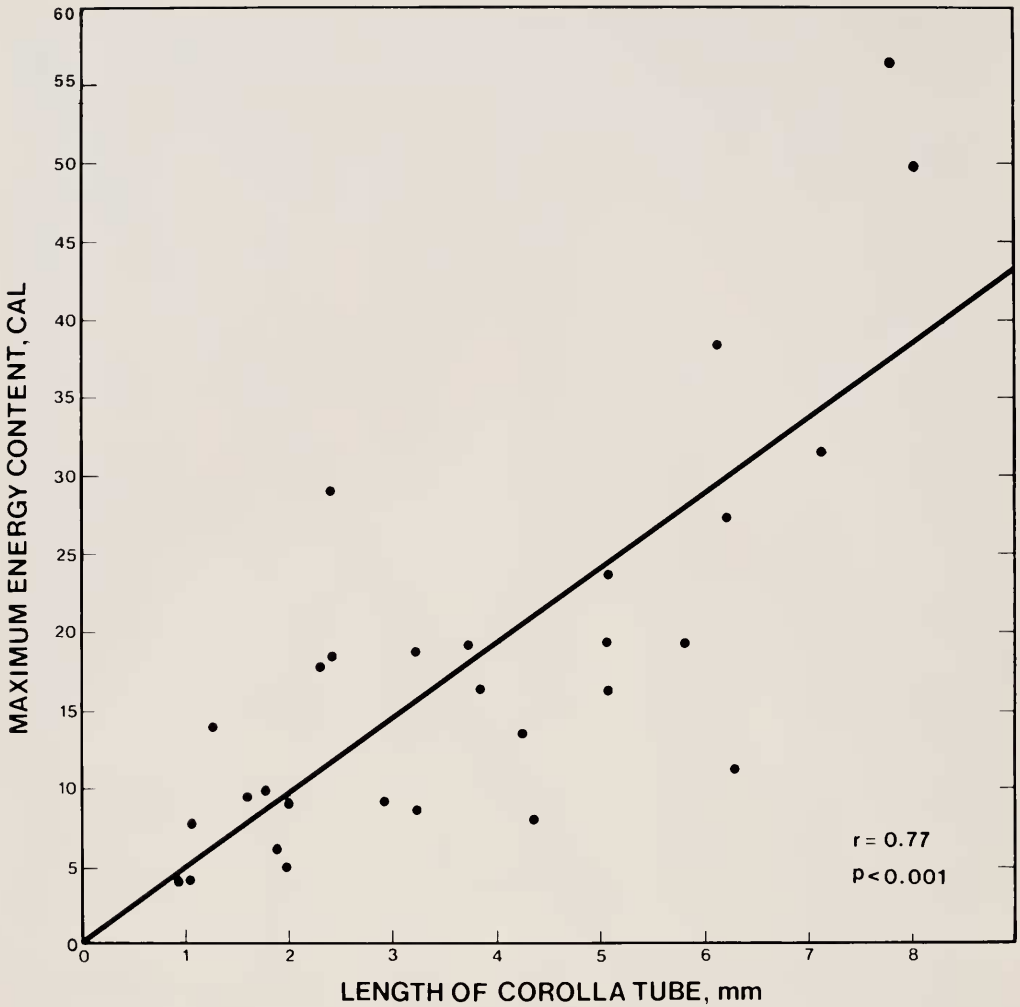


FIGURE 5. Relationship between maximum energy content of nectar and corolla tube length in *Dudleya* subgenus *Dudleya*. Each point represents one population. Linear correlation of $r = .77$ is significant ($P < .001$).

1983) and have been attributed to low temperature and low sunlight. Understandably, the volume of accumulated nectar remains higher and the concentration lower when the weather is cool and humid than when it is warm and dry. The loose fit of the points to the curves in Figure 3 probably results in part from changes in light, temperature, and humidity during our study.

Quantity.—Nectar volume, maximum sugar content, and maximum caloric content vary considerably among species and even among populations in some species. Nectar concentration varies to a lesser extent (Table 1). Field measurements with *D. cymosa cymosa* and *D. brittonii* agree with our greenhouse results.

We find strong positive correlations between maximum nectar volume and corolla tube length ($r = .71$; Fig. 4) and between maximum caloric content and corolla tube length ($r = .77$; Fig. 5). These results suggest that the degree of petal fusion, an important taxonomic character in this genus, has a functional significance. Larger flowers with longer corolla tubes might be expected to require larger pollinators, which require more energy and thus more nectar (Heinrich and Raven 1972) than smaller flowers could hold.

The quantities of sugar offered by the flowers support the hypothesis that most

TABLE 2. Number of living seedlings from self-pollinated flowers and cross-pollinated flowers of *Dudleya*. Thirty seeds from each treatment were sown.

<i>Dudleya</i> species	Time after sowing			
	3 weeks		7 weeks	
	Selfed	Crossed	Selfed	Crossed
<i>brittonii</i>	14	23	8	14
<i>cultrata</i>	29	26	4	22
<i>cymosa marcescens</i>	4	4	2	3
<i>c. ovatifolia</i>	6	2	7	6
<i>ingens</i>	9	3	8	10
2 plants	4	5	3	5
<i>linearis</i>	15	9	7	11

species of *Dudleya* are pollinated by bees and flies, but that some have evolved for pollination by hummingbirds. Nectar accumulates over about three days, with a daily energy production of 2–3 cal/flower/day for most species. These values are similar to some temperate bee-pollinated flowers (Heinrich 1975, 1976, Reader 1977, Rust 1977, Schaffer and Schaffer 1977). Unless insects were excluded from the flowers, the nectar energy would be too small for temperate hummingbirds, which require an intake of 5.5–7.5 kcal/day (Pearson 1954, Stiles 1971), or about 1.5–2.0 g sugar/day (Heinrich 1975). In species that produce large quantities of nectar (up to 7–8 cal/flower/day), the longer corolla tubes, red corolla color, and pendent flower position probably all help prevent feeding by most bees and flies. Although 1000–1500 flowers would be required to support one hummingbird for a day, this number is not inconsistent with some observations (Pearson 1954). Clearly nectar quantities are small enough not to satiate pollinators, and thus small enough to encourage outcrossing, even if several flowers are open simultaneously on each plant (Heinrich and Raven 1972). Nectar concentrations are all within the range typical of both bee- and hummingbird-pollinated species (Hainsworth 1973, Heinrich 1975).

BREEDING SYSTEMS

Phenology of anthesis.—As noted above, *Dudleya* flowers are protandrous (Fig. 1). Anthers and stigmas are initially separated by a few millimeters. About two days after the anthers dehisce, the styles elongate and the stigmas become receptive. As a flower ages, the filaments of its stamens shrivel and the anthers may then contact the stigmas, transferring any remaining pollen. Contact typically occurs four to six days after the flower opens.

Seed set.—All species examined are self-compatible and capable of some auto-fertilization (self-pollination in the absence of pollinators) (Fig. 6). Compared to the other species we investigated, *D. cymosa*, *D. nubigena*, *D. pulverulenta* and one population of *D. brittonii* had high auto-fertility. *D. cymosa* in particular departs from the general morphological pattern in that its stamens form a tight ring around the stigmas deep within the corolla tube, thereby facilitating transfer of pollen as the flowers age.

Except in highly auto-fertile subspecies of *D. cymosa* and in *D. pulverulenta*, mechanical self-pollination produced significantly higher seed set than did auto-fertilization, in most cases by a factor of two or more. Cross-pollinated flowers usually produced nearly twice as many seeds as self-pollinated flowers. Thus, for most species, there is clearly an advantage to attracting pollinators. The increased seed set of outcrossed flowers may be the result of fewer homozygous combinations of deleterious genes (D. A. Levin 1971), or faster pollen tube growth of cross-pollen, resulting in more successful fertilization (Bateman 1956, Smith and Clarkson 1956, Weller and Ornduff 1977).

Seed viability and seedling vigor.—Table 2 shows the number of seedlings present three and seven weeks after sowing 30 seeds each from self- and cross-pollinated flowers of six taxa. There is no significant difference between the number of seedlings from

AVERAGE PERCENT SEED SET BY:

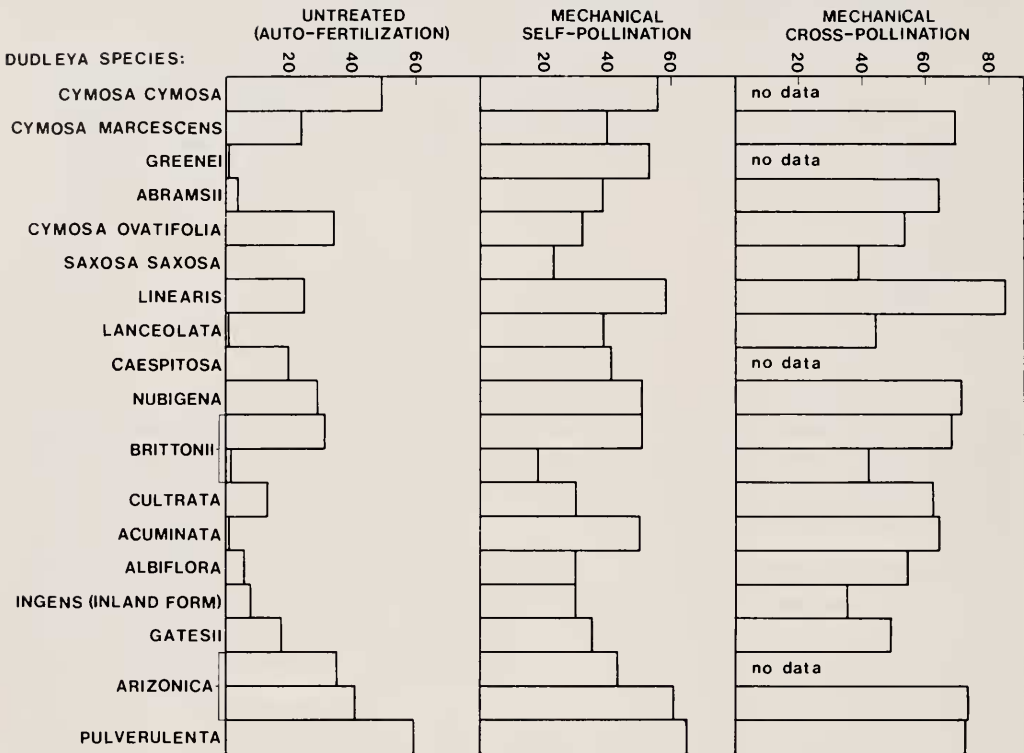


FIGURE 6. Seed set under different treatments in *Dudleya* subgenus *Dudleya*. Species are arranged in order of increasing corolla tube length. Values are means, typically of three flowers each from three different plants.

self-pollinated flowers and cross-pollinated flowers three weeks after sowing (Wilcoxon paired-sample test; $P > .20$). Thus, there appears to be no difference in seed viability. After seven weeks, however, significantly more seedlings survived from cross-pollinated flowers than from self-pollinated flowers ($P < .05$). In contrast, *D. cymosa* showed approximately equal survivorship from the two treatments, suggesting that, like habitually self-pollinating plants, it suffers less inbreeding depression than habitually cross-pollinating species (Grant 1975).

REPRODUCTIVE STRATEGIES

When maximum energy content is plotted against auto-fertility, the species fall into three groups (Fig. 7). First, there is a large group with relatively low auto-fertility (<20%) and moderate to high nectar production. This group contains *D. acuminata*, *D. albiflora*, *D. brittonii*, *D. caespitosa*, *D. cultrata*, *D. gatesii*, *D. greenei*, *D. ingens*, *D. lanceolata*, and *D. saxosa*; *D. bettiniae*, a species whose breeding systems we did not examine, probably also belongs to this group, as do *D. abramsii* and *D. parva*, species in which we had difficulty measuring nectar production. The second group comprises species with relatively high auto-fertility (25–50%) and little nectar (three subspecies of *D. cymosa*, *D. linearis*, and *D. nubigena*), a combination of characters suggesting at least incipient autogamy (Faegri and van der Pijl 1979, Ornduff 1969). Differences between the two groups in both nectar production and auto-fertility are significant (Mann-Whitney test; $P < .001$). The third group consists of the putatively hummingbird-pollinated species (*D. arizonica*, *D. pulverulenta*, and probably *D. anthonyi*, although we did not determine its breeding system).

Our data demonstrate that it is advantageous for most *Dudleya* species to attract

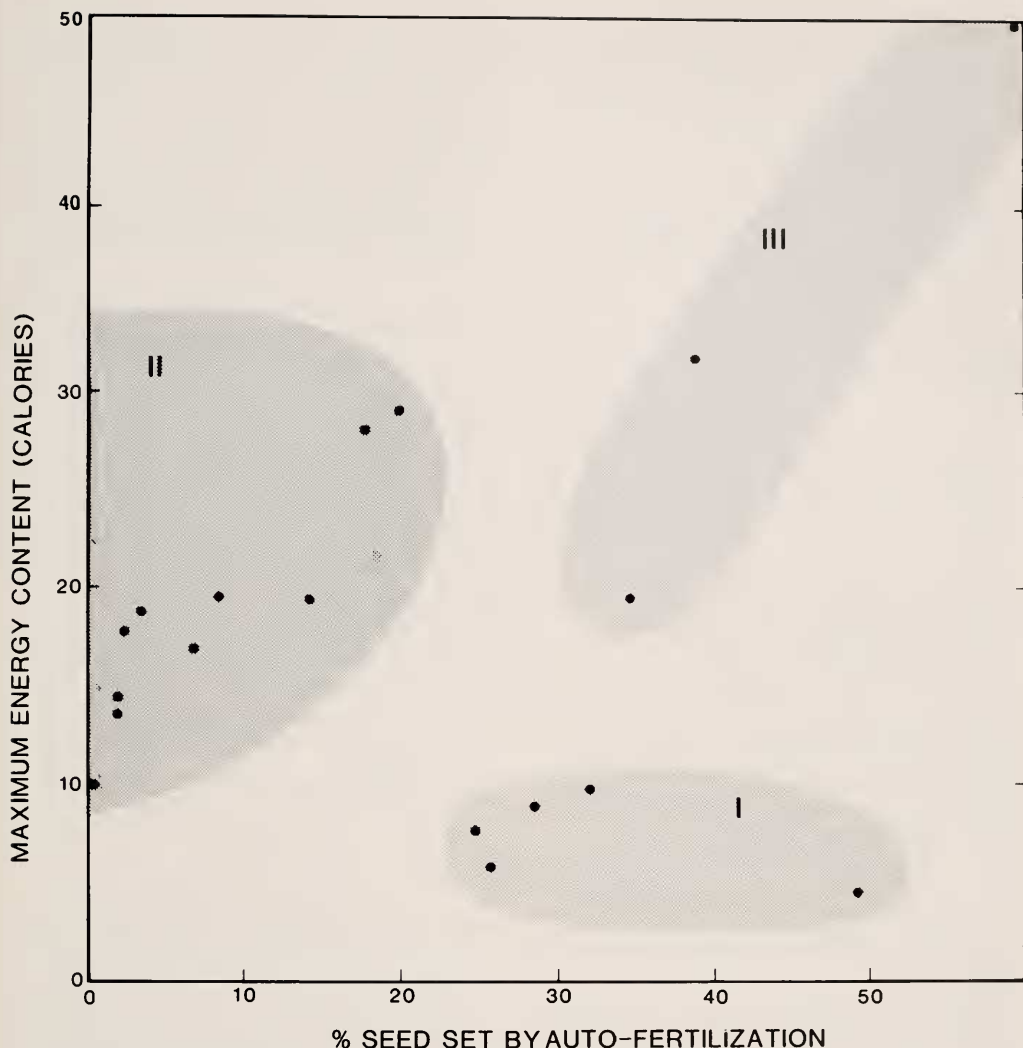


FIGURE 7. Relationship between maximum energy content of nectar and auto-fertility in *Dudleya* subgenus *Dudleya*. Each point represents one population. Species with high auto-fertility produce little nectar (Group I), whereas species with low auto-fertility produce moderate amounts of nectar (Group II). The three populations that do not fit this pattern are hummingbird pollinated (Group III).

pollinators: plants that do so set more seed, whether by self- or cross-pollination. Moreover, there are the immediate advantages to outcrossing of increased seed set and increased seedling vigor, in addition to probable long-term advantages of increased genetic variability (Williams 1975, Solbrig 1976, Gottlieb 1977, Hancock 1977, Solbrig and Rollins 1977).

What then might account for the apparent autogamous tendencies of *D. cymosa* and other members of the group showing high auto-fertility and low nectar production? Unlike the majority of *Dudleya* species, those with this quasi-autogamous syndrome are comparatively short-lived perennial plants growing in habitats with short growing seasons and with great seasonal variation in environmental conditions. *D. cymosa*, for example, is widespread in the Sierra Nevada, Coast Ranges, and Transverse Ranges of California. Conditions that favor autogamy, such as a short and unpredictable reproductive season, small population size, high population turnover, and pollinator unreliability (Grant and Grant 1965, Vasek 1971, Hinton 1976, Hurka et al. 1976,

Solbrig 1976, Solbrig and Rollins 1977) could be expected to be more prevalent in these environments than in the coastal environment typical of most *Dudleya* species. Although we have not tested the relative importance of these factors, unreliable pollination does appear to be involved (G. A. Levin in prep.).

The high auto-fertility of those species pollinated by hummingbirds is, on face value, unexpected. However, preliminary evidence suggests that hummingbirds are unreliable pollinators of *Dudleya*, varying considerably in abundance both temporally and spatially (G. A. Levin in prep.). Increased specialization for hummingbird pollination may concomitantly select for increased ability to set seed in the absence of pollinators.

Even the species with the strongest propensity toward autogamy are protandrous and produce sufficient nectar to attract pollinators. The actual amount of auto-fertilization that occurs in nature depends on the quantity of pollen removed from the anthers before they contact the stigmas, in addition to the auto-fertility of the species (Arroyo 1975). In *Lupinus nanus*, a species with synchronous maturation of anthers and stigma, plants having more than 30% auto-fertility are predominately autogamous (Harding et al. 1974). Field observations indicate that, because of protandry, only about 50% of seed set in *D. cymosa cymosa* results from auto-fertilization in spite of high auto-fertility (G. A. Levin in prep.). *Dudleya* thus has a breeding system that promotes outcrossing while maintaining the possibility of auto-fertilization, the balance being selected according to the particular environment of the species.

In conclusion, this study demonstrates the interdependence of breeding system, pollination syndrome, and reproductive strategy. A short and uncertain growing season and/or pollinator unreliability may make it important to shift the reproductive strategy toward assurance of high seed set. In response, the breeding system is shifted toward greater auto-fertilization, which in turn requires a change in floral morphology and allows lower nectar production—a shift in the pollination syndrome. Thus natural selection does not modify one characteristic of the reproductive system without modifying various other characteristics.

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APPENDIX

Localities of *Dudleya* populations studied

Populations are listed taxonomically in same order as Table 1.

D. abramsii Rose. California, San Diego Co.: Highway 94 5.4 km W of Campo. *D. acuminata* Rose. Mexico, Baja California (Norte): Millers Landing. *D. albiflora* Rose. Mexico, Baja California (Norte): Cedros Island; Highway 1 near Rosarito. *D. anthonyi* Rose. Mexico, Baja California (Norte): Cabo San Quintin. *D. arizonica* Rose. Mexico, Baja California (Norte): Rio Santo Tomas ca. 16 km E of coast; California, San Diego Co.: Campbell Grade, Highway 52 ca. 22 km S of Highway 78; Highway 94 4.8 km W of Campo. *D. bettinae* Hoover. California, San Luis Obispo Co.: Cuyucos. *D. brittonii* Johansen. Glauous form. Mexico, Baja California (Norte): near La Misión; Playa de Punta Banda. Green × glauous form. Mexico, Baja California (Norte): Playa de Punta Banda. *D. caespitosa* (Haworth) Britton & Rose. California, Los Angeles Co.: Topanga Canyon ca. 5 km N of Pacific Ocean; Ventura Co.: Pt. Mugu. *D. cultrata* Rose. Mexico, Baja California (Norte): San Martin Island; Cabo San Quintin. *D. cymosa* (Lemaire) Britton & Rose ssp. *cymosa*. California, Tulare Co.: Hospital Rock, Sequoia National Park. *D. cymosa* ssp. *marcescens* Moran. California, Ventura Co.: Little Sycamore Canyon, Santa Monica Mts. *D. cymosa* ssp. *ovatifolia* (Britton) Moran. California, Los Angeles Co.: Topanga Canyon. *D. gatesii* Johansen. Mexico, Baja California (Norte): Millers Landing. *D. greenei* Rose. California, Santa Barbara Co.: Prisoners' Harbor, Santa Cruz Island. *D. ingens* Rose. Coastal form. Mexico, Baja California (Norte): San Juan de las Pulgas; Punta Cabras. Inland form. Mexico, Baja California (Norte): specific locality unknown. *D. lanceolata* (Nutt.) Britton & Rose. California, Orange Co.: Modjeska Canyon. *D. linearis* (Greene) Britton & Rose. Mexico, Baja California (Norte): West San Benito Island. *D. nubigena* (Brand.) Britton & Rose. Mexico, Baja California Sur: Cabo San Lucas. *D. parva* Rose & Davidson. California, Ventura Co.: Arroyo Santa Rosa. *D. pulverulenta* (Nutt.) Britton & Rose. Mexico, Baja California (Norte): Rancho Arenoso, ca. 50 km E of El Rosario on Highway 1; California, Orange Co.: Laguna Beach. *D. saxosa* (M. E. Jones) Britton & Rose ssp. *saxosa*. California, Inyo Co.: Aguerberry Point, Panamint Mts.